MAYIGRIPHUS ORBUS GEN. ET SP. NOV., A MIOCENE DASYUROMORPHIAN FROM RIVERSLEIGH, NORTHWESTERN QUEENSLAND

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Mayigriphus orbus gen. et sp. nov., an enigmatic Miocene dasyuromorphian from Riversleigh, is described from dental material. The tiny *Mayigriphus orbus* shows a number of derived character-states for Dasyuromorphia and two of these derived features may signify a special relationship with *Planigale* (Dasyuridae). However, no specialised features shown by *M. orbus* are unique to dasyurids within the order and *M. orbus* also possesses derived characters shown by basal thylacinids. Because previous investigation has indicated that Dasyuridae is not currently defined by any dental synapomorphies, caution is demanded regarding allocation of *M. orbus* at the family level. Problems associated with the phylogenetic placement of *M. orbus* portend a story of growing complexity for dasyuromorphian phylogeny — a story progressively being revealed in the Tertiary limestones of Riversleigh. ☐*Mayigriphus, dasyuromorphan, Miocene, Riversleigh.*

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The fossil record for Dasyuromorphia is reviewed by Wroe (1996b, 1997b). Until recently the pre-Pliocene fossil record for Dasyuromorphia was limited to five described taxa, all from deposits in central Australia (*Ankotarinja tirarensis* and *Keeuna woodburnei* (Archer, 1976a), *Wakamatha tasselli* (Archer & Rich, 1979), *Dasylurinja kokuminola* (Archer 1982a) and *Thylacinus potens* (Woodburne, 1967). With the exception of *Thylacinus potens*, investigation has failed to unequivocally link these fossil taxa with elements of modern dasyuromorphian radiations. More recently, the fossil-rich middle to late Tertiary deposits of Riversleigh have yielded six new thylacinid species: *Nimbacinus dicksoni* (Muirhead & Archer, 1990), *Thylacinus macknessi* (Muirhead, 1992; Muirhead & Gillespie, 1995); *Wabulacinus ridei* (Muirhead, 1997), *Ngamalacinus timmulvaneyi* (Muirhead, 1997), *Badjcinus turnbulli* (Muirhead & Wroe, in press), and *Muribacinus gadiyuli* (Wroe, 1996b). However, only two un-named taxa have been assigned to Dasyuridae: a possible phascogaline taxon known from a single M^1 or M^2 (Archer, 1982a) and an un-named 'Antechinus-like' species from Riversleigh (Van Dyck, 1989). Wroe (1996b, 1997b) investigates problems with dasyurid phylogeny, concluding that Dasyuridae is currently defined by possibly three basicranial, but no dental synapomorphies. A new dasyuromorphian described here shows an enigmatic combination of features within Dasyuromorphia and can not be unequivocally assigned at the family level.

Dental nomenclature follows Flower (1867) and Luckett (1993). Taxonomic terminology for Dasyuromorphia follows Wroe (1996b), with three subfamilies recognised within Dasyuridae (Sminthopsinae, Phascogalinae [including *Murexia*], Dasyurinae [including *Neophascogale* and *Phascolosorex*]) and the following taxa considered Dasyuromorphia incertae sedis: *Ankotarinja tirarensis*, *Keeuna woodburnei*, *Wakamatha tasselli* and *Dasylurinja kokuminola*. Higher level marsupial systematics follows Marshall et al. (1990). Material is housed in the Queensland Museum (QMF).

SYSTEMATICS

Order DASYUROMORPHIA Gill, 1872
Family INCERTAE SEDIS

Mayigriphus gen. nov.

TYPE AND ONLY SPECIES. *Mayigriphus orbus* gen. et sp. nov.

GENERIC DIAGNOSIS. *Mayigriphus orbus* differs from all dasyurids in the following combination of features: Premolar row compressed longitudinally, P_1 very small; P_3 reduced but with two roots; M_1 compressed on long axis with protoconid central on long and transverse axes with paraconid tiny; M_{1-4} metaconids and metacristids reduced; M_1 metaconid not differentially reduced relative to M_{2-4} metaconids;

lingual anterior termination of cristid obliqua on M_{1-4}, with M_3 cristid obliqua terminating beneath metacristid carnassial notch; M_{1-4} protoconids lingually shifted and recurved; M_{1-3} entoconids small to tiny, M_4 talonid reduced with entoconid absent. *Mayigriphus orbus* can be distinguished from known thylacinids by the following combination of features: M_1 shows a greatly reduced paraconid but only moderately reduced metaconid; clearly defined hypoconulid notch in anterior cingulid of lower molars; very small size; reduction of P_3 relative to P_2; lack of diastema between P_1 and P_2. Mayigriphus orbus differs from known bandicoots in possession of the above combination of characters, a well-defined posterior cingulid and more buccally shifted hypoconulid.

ETYMOLOGY. Wanyi *mayi*, tooth; Latin *griphus*, puzzle; refers to the enigmatic combination of dental features. Masculine.

Mayigriphus orbus sp. nov.
(Fig. 1)

ETYMOLOGY. Latin *orbus*, orphan, refers to its uncertain phylogenetic position.

MATERIAL. Holotype, QMF23780, right dentary with partial anterior alveolus of P_1, P_1 posterior root, P_{2-3}, M_{1-4}; Paratype QMF22791, right dentary fragment containing M_3 and alveolus for M_4. All from early late Miocene Encore Site, Riversleigh.

DESCRIPTION. Dentary broken away anteriorly from midpoint of P_1 anterior root alveolus and posteriorly from about 1mm along ascending ramus; dentary almost uniform in depth, slight tapering anteriorly from beneath P_3 protoconid; mental foramen beneath M_1 hypoconid.

P_1. P_1 crown missing, only posterior half of anterior root alveolus and posterior root remain; based on root and alveolus size P_1 small, less than half P_2 length; anterior alveolus buccally displaced.

P_2. No diastema between P_1 and P_2; twin rooted; P_2 largest premolar in height and length; protoconid moderately worn; buccal cingulid runs posteriorly from midpoint between anterior and posterior roots to small posterior central cuspule on heel; another cingulid circumscribes the lingual crown base from this cuspule to anterior margin of posterior root.

P_3. no diastema between P_2 and P_3; twin rooted; P_3 morphology similar to P_2 but differs in possession of continuous cingulid circumscribing base of entire crown and smaller size (P_3 around 30 percent smaller in height an length).

M_1. no diastema between P_3 and M_1; M_1 unworn; principal cusps in order of decreasing height; protoconid, metaconid, paraconid, hypoconid and entoconid; entoconid tiny, closely abutting posterior face of trigonid adjacent to metaconid; paraconid damaged, but from basal dimensions was clearly small; metaconid small and shifted posteriorly; protoconid dominant cusp, lingually recurved, occupying almost central position on tooth; M_1 reduced on the long axis; talonid small, slightly wider transversely than trigonid but shorter on long axis; paracristid parallel to, and cristid obliqua shows slight lingual inflection at anterior end; metacristid and hypocristid parallel and angled at about 20° to transverse axis of dentary; cristid obliqua terminates beneath apex of protoconid; anterior cingulid runs basally from paraconid to beneath protoconid; posterior cingulid weakly developed.

M_2. M_2 differs from M_1 as follows; M_2 much larger; paraconid much larger; metaconid relatively and absolutely lager though still small compared to protoconid; talonid shorter on long axis; cristid obliqua terminates against posterior face of trigonid in more lingual position, with angle formed between cristid obliqua and hypocristid more acute; metacristid and hypocristid run closer to transverse axis of dentary; entoconid relatively larger than in M_1 though still small; posterior cingulid more strongly developed; M_2 paracristid runs at about 30° to long axis of dentary, with angle between paracristid and metacristid slightly less than 90°.

M_3. M_3 differs from M_2 as follows; protoconid larger; on transverse axis trigonid wider and talonid shorter; entoconid on M_3 smaller; cristid obliqua terminates in a more lingual position against posterior face of trigonid beneath carnassial notch of metacristid.

M_4. M_4 similar to M_3 except: metaconid smaller than paraconid; protoconid less lingually recurved; talonid greatly reduced, entoconid absent, hypoconid and hypoconulid small; no posterior cingulid.

Meristic gradients from M_{1-4}. orientation of metacristid and hypocristid to long axis of dentary increasingly transverse from M_{1-2}, departs away from transverse from M_{2-3}, then back to more transverse orientation from M_{3-4}; orientation of paracristid to long axis of dentary increas-

FIG. 1. *Mayigriphus orbus* sp. nov., QMF23780, holotype. A, buccal view. B and D, stereo-pair, occlusal view of M_{1-4}. C and E, stereo-pair, occlusal view of P_1 posterior alveolus, P_{2-3}, M_{1-4}.

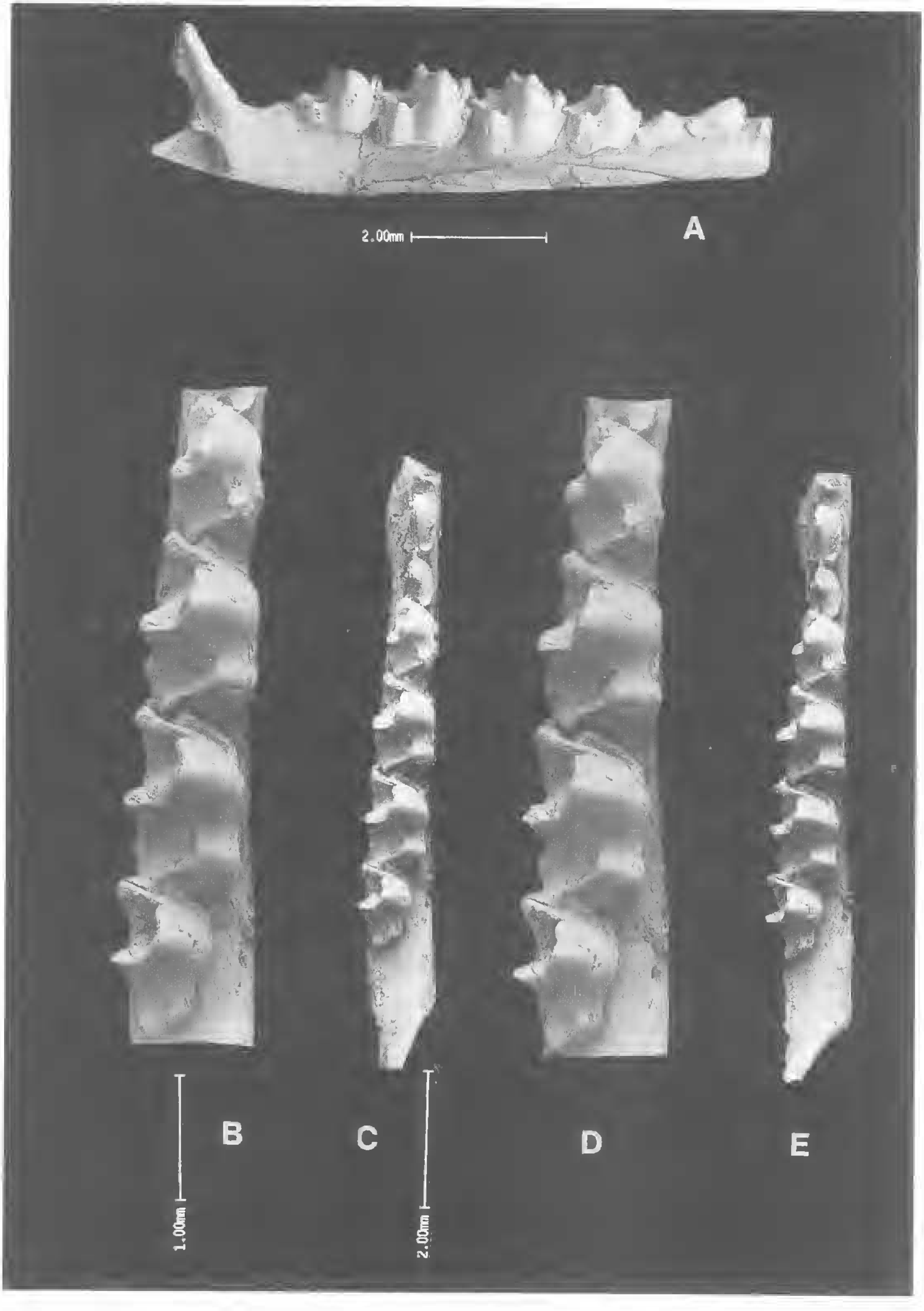
2.00mm
A
B
C
D
E
1.00mm
2.00mm

TABLE 1. *Mayigriphus orbus*, dental measurements (mm). l=anteroposterior dimension, w1=maximum transverse dimension of trigonid, w2=maximum transverse dimension of talonid.

Ref. no	P_2		P3		M_1			M_2			M_3			M_4		
	len	wid	len	wid	l	w1	w2	l	w1	w2	l	w1	w2	l	w1	w2
QMF 23780	0.83	0.42	0.67	0.36	1.26	0.64	0.67	1.49	0.84	0.86	1.52	0.84	0.78	1.33	0.74	0.42
QMF 22791											1.45	0.86	0.68			

ingly transverse from M_{1-3}, termination of cristid obliqua against posterior face of trigonid increasingly lingual M_{1-4}; reverses departing from transverse for M_{3-4}; protoconid and metaconid height increases M_{1-3}, decreases M_{3-4}; paraconid height increases M_{1-4}; talonid width increases M_{1-2}, decreases M_{3-4}.

CHARACTER ANALYSIS

Wroe (1996b, 1997b) discusses taxa considered appropriate in the reconstruction of a dasyuromorphian morphotype (i.e., peradectids, didelphoids, microbiotheriids, peramelemorphians). Similar methodology is used for characters treated here to assess character-state polarities (Tables 2, 3). Within Dasyuromorphia *Ankotarinja tirarensis* is the least derived taxon and a possible outgroup to remaining dasyuromorphians. *Muribacinus gadiyuli* and *Badjcinus turnbulli* are the least derived thylacinids. For Dasyuridae the following taxa are considered plesiomorphic for their respective subfamilies: *Murexia longicaudata* (Phascogalinae), *Neophascogale lorentzii* (Dasyurinae) and *Sminthopsis leucopus* (Sminthopsinae).

P_3. A P_3 larger than P_2 is plesiomorphic for outgroups to Dasyuromorphia (Wroe, 1996b, 1997b). For *A. tirarensis* P_3 is slightly smaller than P_2. *Wakamatha tasselli* shows P_3 larger than P_2. The basal thylacinid *Badjcinus turnbulli* has P_3 slightly smaller than P_2. Wroe (1996b) interprets similar P_3 morphology for *Muribacinus gadiyuli* on the basis of alveolar dimensions. For all remaining thylacinid taxa P_3 is larger than P_2, with the largest P_3 in the most derived taxa (*Thylacinus*). Within Dasyuridae wide variation is apparent for this feature. Taxa treated here as basal to their respective subfamilies show a P_3 larger than P_2 (*Murexia*, *Sminthopsis leucopus*), or slightly reduced (*Neophascogale*). However, within each subfamily some taxa show marked reduction or absence of P_3. P_3 reduction in *Mayigriphus orbus* exceeds that shown by all taxa considered Dasyuromorphia incertae sedis, all Thylacinidae and basal taxa for dasyurid subfamilies.

M1 paraconid. The M_1 paraconid is not reduced in dasyuromorphian outgroups and *A. tirarensis*, *W. tasselli*, moderate reduction is shown by thylacinids (excepting *B. turnbulli* which shows marked reduction) and plesiomorphic Sminthopsinae (*Sminthopsis leucopus*), Phascogalinae (*Murexia*) and Dasyurinae (*Neophascogale*). M_1 paraconid reduction in *M. orbus* is less marked than in all Dasyurinae excepting *Neophascogale*. For *M. orbus* M_1 shows greater reduction of the paraconid than for all Phascogalinae and Sminthopsinae except *Planigale*.

M_4 talonid. The M_4 talonid is unreduced in basal taxa for Dasyuromorphian outgroups except bandicoots (e.g., *Yarala burchfieldi*, Muirhead & Filan, 1995). Within Dasyuromorphia *A. tirarensis*, basal phascogaline (*Murexia*) and dasyurine (*Neophascogale*) taxa show slight reduction for this feature. The M_4 talonid is greatly reduced on the plesiomorphic dasyuromorphian condition for *W. tasselli*, most dasyurines and phascogalines, and all sminthopsines. For thylacinids the M_4 talonid is unreduced for basal taxa (*Muribacinus*, *Badjcinus*), but significantly reduced for derived species (*Thylacinus*, *Wabulacinus*). Even for specialised *Thylacinus* M_4 talonid reduction does not approach that of derived dasyurids which show far greater diminution on the transverse axis. The degree of reduction for this feature in *M. orbus* is closest to that shown in *Phascogale*, but less than for most Dasyurinae, and all Sminthopsinae.

Cristid obliqua orientation. A buccal position for the anterior termination for the cristid obliqua relative to the carnassial notch of the metacristid is common to most dasyuromorphian outgroup taxa. This feature is associated with cristid obliqua orientation and formation of a right angle between the cristid obliqua and hypocristid. Most outgroup taxa to Dasyuridae and Thylacinidae show a cristid obliqua aligned closely with the long axis of the dentary and a 90° angle is formed between the cristid obliqua and hypocristid. In the character-analysis (Table 2) only M_3 is considered. Buccal termination is shown by *A. tirarensis* and, to a lesser degree, by *K. woodburnei* and *W. tasselli*. Basal thylacinids show relatively lingual anterior termination for the cristid obliqua, but a more buccal position is apparent in *Thylacinus*. Basal dasyurines show lingual termination for the cristid obliqua (*Neophascogale*, *Myoictis*, *Dasyurus hallucatus*), but more specialised taxa show buccal termination (other *Dasyurus*, *Dasycercus*, *Dasyuroides*, *Sarcophilus*). All phascogalines show lingual termination. Sminthopsines show buccal termination. *Mayigriphus orbus* shows lingual termination.

Orientation of the cristid obliqua correlates with other features of both the upper and lower molars. These include the angle between the postparacrista and premetacrista (together termed the centrocrista), the relative size of the protoconid and metaconid and, the occlusal surface area presented by the protocone and talonid basin. Scoring of character states for cristid obliqua without consideration of these associated features may be phylogenetically misleading. For example, derived *Thylacinus* and some dasyurines show longitudinal alignment for the M_3 cristid obliqua (unspecialised didelphids, microbiotheriids and *A. tirarensis)*, but for these derived dasyuromorphians this feature correlates with protoconid hypertrophy, metaconid reduction or loss, and a linear centrocrista. These character-states are all associated with the dominance of longitudinally oriented vertical shearing crests.

The basal position for Sminthopsinae within Dasyuridae indicated by molecular analyses (Kirsch et al, 1990; Krajewski et al., 1993; 1994) supports the contention that a buccal point of termination for the cristid obliqua is a plesiomorphy for the clade. However, dental features of Sminthopsinae are products of a different selective regime and transverse rather than longitudinal vertical shearing crests dominate. Archer (1976) noted that a buccal position for the cristid obliqua may be associated with reduction of the paracone or a lingual shift in the carnassial notch (of the metacristid). Both derived features are shown by sminthopsines and it is probable that cristid obliqua position represents a correlated apomorphic feature. A further derived feature shown by sminthopsines is gross reduction of the talondis on the anteroposterior axis which may also impact on cristid obliqua orientation. For sminthopsines and derived dasyurines and thylacinids, a buccal position for the cristid obliqua is treated as derived relative to that of microbiotheriids, unspecialised didelphids, bandicoots and *A. tirarensis* (Tables 2, 3). A relatively more lingual termination for the cristid obliqua, as shown by most dasyurids and basal thylacinids, is also considered derived. The character complex associated with most dasyurids (a relatively lingual anterior termination point and acute angle formed between the cristid obliqua and hypocristid) is scored as 'a'. Buccal termination and formation of 90° between the cristid obliqua and hypocristid may be associated with increased transverse vertical shear (b) or increased longitudinal vertical shear (c).

Angle between paracristid and metacristid. For dasyuromorphian outgroups an acute angle is formed between the paracristids and metacristids (mirrored by an equivalent angle formed between the postmetacristae and preprotocristae with which they occlude in the upper dentition). Similar morphology is shown by *A. tirarensis*, *W. tasselli* and sminthopsine dasyurids. All dasyurines, phascogalines, basal thylacinids for which a metacristid is retained, and *M. orbus* show a relatively obtuse angle between paracristids and metacristids. Widest paracristid-metacristid angles are in *Sarcophilus*, *Glaucodon* and *D. maculatus* among dasyurids and *Ngamalacinus* among thylacinids. This phenomenon is correlated with carnivory and the development of longitudinally aligned vertical shearing crests.

Hypoconulid notch. Many marsupials have a distinct notch in the anterior cingulae of their lower molars to receive the hypoconulid of the preceding tooth. Outgroup data for Dasyuromorphia regarding this feature is equivocal. Some outgroup taxa (e.g., some peradectids) show a well-developed hypoconulid notch, but among other possible outgroups this feature is absent (e.g., peramelemorphs). Within Dasyuromorphia this feature is well-developed for *Ankotarinja tirarensis* and *Keeuna woodburnei*, but poorly defined for *Wakamatha tasselli* (see Wroe (1996b) re arguments for possible bandicoot affinities of this taxon). Among thylacinids, a well-developed hypoconulid notch is present for *Muribacinus* and *Badjcinus*, weakly-defined in *Ngamalacinus*, and absent in all other taxa. A well-developed hypoconulid notch occurs in all dasyurids excepting *Dasyurus maculatus* (reduced), and *Glaucodon* and *Sarcophilus* (absent). *Mayigriphus orbus* has a well-defined hypoconulid notch. Wroe (in press b) infers that loss of the hypoconulid notch is a function of ad-

TABLE 2. Characters and character-states used in phylogenetic analysis.

C1. P_3 size relative to P_2. 0. larger. 1. reduced. 2. intermediate. 3. tiny. 4. absent.
C2. M_1 paraconid size. 0. large. 1. reduced. 2. tiny. 3. absent.
C3. M_4 talonid size. 0. large. 1. moderately reduced. 2. markedly reduced. 3. tiny.
C4. M_3 cristid obliqua morphology *. P. plesiomorphic. a. lingual. b. trans. shear. c. long. shear.
C5. Angle between paracristid-metacristid. 0. acute. 1. intermediate. 2. obtuse.
C6. Hypoconulid notch. 0. well developed. 1. intermediate. 2. absent.
C7. Metaconid morphology. 0. no clear differential between M1 and M2-4. 1. clear differential.
C8. M_{2-4} metaconid size. 0. large. 1. reduced. 2. greatly reduced. 3. absent.
C9. M_3 entoconid size. 0. large. 1. reduced. 2. absent.
* Three derived states recorded for this character (see text).

vanced carnassialisation for derived dasyurids and thylacinids, noting that the shift to a predominance of longitudinal vertical shear in marsupial carnivores diminishes the requirement for a brace against transverse forces (i.e., the likely role for the hypoconulid notch).

Archer (1982b) regarded a hypoconulid notch in the anterior cingulum as a possible dasyurid synapomorphy. But Wroe (1997) concludes that it may have been in the common ancestor of Dasyuromorphia and was almost certainly in the common ancestor of Dasyuridae-Thylacinidae. For specialised dasyurids (*Sarcophilus* and *Glaucodon*) and thylacinids (*Thylacinus*, *Wabulacinus*) loss of the hypoconulid notch correlates with advanced carnassialisation.

Metaconid . A well-developed metaconid on all lower molars occurs in all putative Dasyuromorphian outgroups. The same is so for *A. tirarensis*, *K. woodburnei* and *W. tasselli*. All thylacinids show marked reduction or loss of the metaconid on all lower molars. Among Dasyuridae this feature is variable. Plesiomorphic taxa for each subfamily show no reduction of the metaconids. However, specialised Dasyurinae and Sminthopsinae show derived character-states. Derived dasyurines show a reduced M_1 metaconid, but less reduction for M_{2-4} metaconids (*Dasycercus*, *Dasyuroides*, *Dasyurus*, *Sarcophilus*). In *Planigale* metaconid diminution is less advanced on M_1 and more uniform through M_{2-4}. This phenomenon shown for *Planigale* is also common to thylacinids which retain metaconids (except *Badjcinus turnbulli* which shows the typical dasyurine condition). *Mayigriphus orbus* shows uniform reduction of M_{1-4} metaconids, the character-state common to *Planigale* among dasyurids and *Muribacinus*, *Nimbacinus* and *Ngamalacinus* among thylacinids.

Localised metaconid reduction (i.e., a clear differential shown between M_1 and M_{2-4} metaconid reduction) as shown by some dasyurines, sminthopsines and *Badjcinus*, is probably related to brachycephalisation, shortening of the tooth row on the anteroposterior axis and concomitant premolarisation of M_1 (Archer, 1976). Generalised metaconid reduction (M_{1-4}) correlates with increased size of the protoconid and primacy of the paracristid and postmetacristae in vertical shear. For carnivorous dasyurids and thylacinids these derived features are associated with alignment of the vertical shearing crests with the long axis of the tooth row.

Entoconid. Large entoconids are plesiomorphic for dasyuromorphian outgroups, *A. tirarensis*, *K. woodburnei*, basal dasyurines and sminthopsines, and phascogalines. Entoconids are reduced or absent in some *Sminthopsis* and *Antechinomys* among sminthopsines and *Parantechinus*, *Pseudantechinus*, *Dasyuroides*, *Dasycercus*, *Dasykaluta*, most *Dasyurus* (excepting *D. hallucatus*), *Sarcophilus* and *Glaucodon*. All thylacinids show some entoconid reduction, with the least reduction in *Muribacinus* and the greatest by *Thylacinus*. *Mayigriphus orbus* shows moderate reduction for this feature. Archer (1981) and Sanson (1985) note that no clear form-function relationship explains the distribution of entoconid reduction and loss among dasyurids, but note that this reduction is greatest for arid-adapted species (some *Sminthopsis*, *Antechinomys*, *Dasyuroides*, *Dasycercus*) However, considerable reduction or loss is shown for some species found in less extreme environments and for large dasyurid and thylacinid carnivores this phenomenon is likely associated with carnivory. More form-function data is required here.

TABLE 3. Character/taxon matrix.

Mayigriphus orbus	211a2	0011
Alphadon marshi	00000	0000
Marmosa sp	00000	0000
Didelphis marsupialis	10000	0000
Dromiciops australis	00100	1000
Yarala burchfieldi	00200	2000
Ankotarinja tirarensis	10000	0000
Keeuna woodburnei	???a1	0?00
Wakamatha tasselli	0?200	1?00
Muribacinus gadiyuli	110a2	0010
Badjcinus turnbulli	110a2	0110
Nimbacinus dicksoni	?01?2	?01?
Ngamalacinus timmulvaneyi	?01c1	1020
Wabulacinus ridei	0??c2	1?22
Thylacinus macknessi	001c?	1?31
Thylacinus cynocephalus	002c2	1032
Sminthopsis leucopus	102b0	0002
Planigale maculata	213b0	0012
Planigale gilesi	313b0	0012
Planigale tenurostris	213b0	0012
Murexia longicaudata	011a1	0000
Phascogale tapotafta	101a1	0000
Neophascogale lorentzii	101a1	0000
Myoictis melas	121a1	0000
Parantechinus apicalis	223c1	0102
Dasyurus hallucatus	322a1	1110
Daysurus maculatus	322c2	2121
Sarcophilus harrisii	323c2	2121

DISCUSSION

BIOSTRATIGRAPHY AND ECOLOGY. To date *M. orbus* is restricted to early late Miocene Archer et al. (1995) Encore Site at Riversleigh. Encore has produced a fauna that includes several unique taxa, including a large dasyuromorphian of uncertain affinity (unpubl. data), a giant *Ekaltadeta* (Wroe, 1996a), a derived koala (Black, pers. comm.), a palorchestid structurally intermediate between species from Riversleigh System C and the late Miocene *Palorchestes painei* of Alcoota (Black, 1997) and a *Warenja*-like wombat (Archer et al., 1995). The rootless teeth of this wombat (unknown for other species at Riversleigh) and the relatively low abundance of the frog *Lechriodus intergervis*, common in other Miocene Riversleigh deposits (Godthelp, pers. comm.) indicate that climatic conditions may have been drier for the depositional episode during which Encore was produced. Tentative support for a relatively late age for Encore site, is also forwarded by Wroe (1997a). If *M. orbus* is a dasyurid then the derived dentition (relative to other Miocene dasyurids) might also suggest a late age for Encore site. As noted above for small dasyurids, circumstantial evidence correlates entoconid reduction with adaptation to relatively dry environments.

Mayigriphus orbus is the smallest dasyuromorphian from the Oligocene and Miocene of Riversleigh and is comparable to *Planigale maculatus* in size. Only one other marsupial insectivore has been identified that might have competed closely with *M. orbus*, the diminutive bandicoot *Yarala burchfieldi* (Muirhead, 1995). As with modern *Planigale* (Denny, 1982) the diet of *M. orbus* probably included invertebrates, frogs, small lizards and/or small mammals.

PHYLOGENY. *Mayigriphus orbus* shows a unique mosaic of features among dasyuromorphians. Two features of *M. orbus* may indicate a relationship with *Planigale* (the greatly reduced M_1 paraconid concurrent with a moderately reduced M_1 metaconid, and relatively uniform diminution of the M_{1-4} metaconids). Although a comparable degree of M_1 paraconid reduction is also common to many derived dasyurines (e.g., *Pseudantechinus*), in these taxa diminution of the M_1 metaconid is far more advanced and a clear differential is produced between that shown by M_1 and M_{2-4}. Additional apomorphies shared by *M. orbus* and *Planigale* (e.g., reduction of M_4 talonid, entoconid and P_3), are also found in other specialised dasyurid taxa. On the basis of cytochrome-b data, Painter et al. (1995) estimate the oldest branchings within *Planigale* at 11-15 mya, thus the possibility that *M. orbus* represents an early branch of this radiation can not be discounted. However, *M. orbus* shows at least 2 derived features not in *Planigale* (wide angle formed between the paracristid, metacristid, a buccal shift in the point of termination of the cristid obliqua). The oldest material clearly attributable to *Planigale* is Pliocene (Archer, 1982a). Based on available data, a sister taxa association for *M. orbus* with *Planigale* is considered equivocal.

Even at the family level, the phylogenetic position of *M. orbus* is considered uncertain, because it has a number of features that might be interpreted as synapomorphies for either derived dasyurid or thylacinid clades, but no unequivocal synapomorphies (within Dasyuro morphia) for either family. Two synapomorphies for the Dasyuridae are in the lower dentition of *M. orbus*: reduction of P_3 (Tate, 1947; Archer, 1982b; Marshall, 1990) and the hypoconulid notch in the lower molars (Archer, 1982b). Status of both as shared-derived features for Dasyuridae is questioned by Wroe (1996b, 1997b). Reduction of P_3 is certainly common within Dasyuridae which culminates in the loss of this tooth among specialised taxa. However, reduction or loss of P_3 may have occurred independently at least 3 times in the Dasyuridae (Archer, 1981). A further argument against the phylogenetic value of this character at the family level is the P_3 smaller than P_2 in 2 thylacinids from Riversleigh (Muirhead & Wroe, in press; Wroe, 1996b, 1997b). The status of the hypoconulid notch as a shared derived feature for dasyurids has been undermined by the discovery of plesiomorphic thylacinids with a well-defined hypoconulid notch in the lower molars (Wroe, 1997b; Muirhead & Wroe, in press). Marked reduction of the M_1 paraconid in *M. orbus* is common to specialised dasyurids but not thylacinids, excepting *Badjcinus turnbulli* (Muirhead & Wroe, in press). None of these features represent unequivocal synapomorphies for Dasyuridae and each have been independently derived within specialised dasyurid lineages. At least 3 features in *M. orbus* suggest a possible alliance with thylacinids. Firstly, the lack of a clear differential between metaconid reduction on M_1 and M_{2-4} in *M. orbus* is known only for *Planigale* among dasyurids but common to plesiomorphic thylacinids. In all dasyurids except *Planigale*, M_1 metaconid reduction clearly exceeds that of M_{2-4}. Although reduction of the M_{2-4} metaconids is less pronounced in *M. orbus* than in known thylacinids, excepting *Muribacinus*, it is greater than for most dasyurids except *D. maculatus*, *Sarcophilus* and *Planigale*. Secondly, the wide angle formed between the paracristid and metacristid in *M. orbus* is found in basal thylacinids, but only *D. maculatus*, *Sarcophilus* and *Glaucodon* among dasyurids. Thirdly, among specialised dasyurids, reduction of the M_{1-4} talonids and metaconids is commonly associated with a buccal shift in the point of termination of the cristid obliqua. In both *M. orbus* and plesiomorphic thylacinids this is not the case, with the cristid obliqua terminating in a relatively lingual position. Ultimately, this may be related to Ride's (1964) observation of a difference between *Thylacinus* and specialised dasyurids in the composition of the principal posterior shearing crest. Ride pointed out that, in *Thylacinus*, the posterior shearing crest runs from the protoconid directly to the hypoconid, while in derived dasyurids (especially *Sarcophilus*) the posterior shearing crest connects the protoconid and metaconid.

CONCLUSIONS

If *M. orbus* is a dasyurid it represents the most derived member of the family known from pre-Pliocene times, with the possible exception of the Miocene *Dasylurinja kokuminola* (Archer, 1982a) from Lake Yanda in central Australia. A special relationship between these two taxa can not be discounted, with both showing specialisations associated with carnassialisation (the much larger size of *D. kokuminola* precludes the possibility that the 2 taxa are conspecific). *D. kokuminola* is known only from a single upper molar and direct comparisons with *M. orbus* cannot be made. Among known dasyurids *M. orbus* shares the greatest number of derived features with *Planigale*: two character-states (disparate reduction of the M_1 paraconid and metaconid and uniform reduction of the M_{1-4} metaconids) suggest the possibility of a special relationship for the 2 taxa. However, uniform diminution of the M_{1-4} metaconids is also shown by some basal thylacinids.

Mayigriphus orbus shows no unequivocal synapomorphies for either dasyurid or thylacinid clades. For Dasyuridae, unique derived-features (within Dasyuromorphia) are only found in the basicranium (Wroe, 1996b, 1997b). Unique derived features (within Dasyuromorphia) uniting Thylacinidae have been identified only in the upper dentition (Wroe, 1996b). Neither region is known for *M. orbus*. Confident phylogenetic assignment for *M. orbus* has been further tempered by the identification of possible thylacinid apomorphies in this taxon, which must be considered in the following context: investigation of Oligocene and Miocene material from Riversleigh is revealing a complex dasyuromorphian phylogeny dominated by a diverse thylacinid clade, showing greatly expanded intrafamilial variation (Muirhead, 1992, 1997; Muirhead & Archer, 1990; Muirhead & Wroe, in press; Wroe, 1996b, 1997b) a close relationship between Dasyuridae and Thylacinidae has been established by molecular studies (Lowenstein et al., 1981; Sarich et al., 1982; Thomas, 1989; Krajewski et al., 1992), and a relatively recent genesis for Dasyuridae has been suggested (Archer, 1982a; Krajewski, 1992; Wroe, 1996b, 1997b). Given this emerging climate of complexity for dasyuromorphian phylogeny, the curious mix of derived features in *M. orbus* (otherwise considered diagnostic of either specialised dasyurid or thylacinid clades) makes reliable placement within either family impossible, particularly as this decision must currently be based solely on elements of the lower dentition. Problems associated with determining the phylogenetic position of *M. orbus* highlight an unexpected phylogenetic scenario. Despite an abundance of dasyuromorphian material from Oligocene-Miocene deposits of Riversleigh no taxon has yet been described which can be unequivocally associated with elements of the now ubiquitous dasyurid radiation.

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